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Nutrient Response of Water Hyssop to Varying Degrees of Soil Saturation

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ABSTRACT

Tissue concentrations of nitrogen (N) and phosphorus (P) were measured in water hyssop (*Bacopa monnieri*) subjected to four progressive levels of flooding: well-drained Control, Intermittently Flooded, Partially Flooded, and Continuously Flooded. Soil redox potential (Eh), measured at two levels in the mesocosms decreased under flooding. Flooding increased biomass and decreased root growth and N and P concentrations in shoots, with the decreases being most pronounced in the Partially Flooded and Continuously Flooded treatments. The decreased uptake of N and P under flooding underscores the need to better understand how wetland plants function in nutrient-rich environments subjected to variable flooding. Additionally, the apparent decreased translocation of N and P from the root to the shoot in flooding conditions may be indicative of an overall decrease in mineral transport, which would have implications for the design and management of remediation systems.

Keywords: nitrogen, phosphorus, nutrient uptake, environmental stresses, water quality

INTRODUCTION

When the land surface is inundated with stagnant water, oxygen diffusion into the soil is limited, resulting in a series of step-wise chemical reductions. Trends in oxidation/reduction reactions may be estimated by soil redox potential (Eh),

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with lower Eh designating more reducing conditions. Under standard conditions (25°C and pH = 7) bioavailable oxygen is depleted at Eh = +350 mV. Soil microorganisms then utilize alternate electron acceptors, such as nitrate, manganese, and iron, resulting in further soil reduction (Ponnamperuma, 1984; Gambrell and Patrick, 1978). These changes can decrease the bioavailability of some plant nutrients, such as nitrogen (N), while increasing others such as iron to detrimental levels (Farmer et al., 2005).

Terrestrial plants subjected to soil reduction must undergo a number of metabolic and morphological changes to acclimate to anoxia and the associated toxins. Initially, metabolic responses in the root system result in diminished root function (Gibbs and Greenway, 2003; Greenway and Gibbs, 2003), followed by decreased leaf gas exchange (Pezeshki, 2001). The combination of decreased carbon assimilation and a short-term increase in respiration, often compounded by productions of toxins in reduced soils, results in mortality of flood-sensitive plants. Flood-insensitive plants respond to root anoxia by forming semi-continuous gas conduits in the cortex (lacunae), allowing diffusion of oxygen from the shoot into the rhizosphere (as reviewed by Armstrong and Drew, 2002; Pezeshki, 2001; Evans 2003), somewhat ameliorating the effects of flooding. Under persistent reducing conditions, however, even wetland plants may show long-term stress responses, such as decreased growth and nutrient uptake, and damage to photosynthetic systems (Pezeshki, 2001).

Water hyssop (*Bacopa monnieri*) has a pan-tropical distribution and is a common species in wetlands near the Gulf of Mexico, forming a common component of marsh communities in areas that are sporadically subjected to flooding and salt stress during storm events (Visser et al., 1998). Hurricane Camille, which made landfall near the mouth of the Mississippi River in August of 1969, devastated a number of marsh species; however *B. monnieri* was largely unaffected (Chabreck and Palmisano, 1973). *B. monnieri* seeds are not highly viable (Tiwari et al., 2001); the plant requires bare ground to become established (Shah, 1965 from Tiwari 2001). If nutrients are adequate, *B. monnieri* can quickly colonize bare marsh soils, becoming a major component of the flora (Dalrymple et al., 2003), even in waters subjected to agricultural and industrial pollution (Gupta, 2003).

B. monnieri is considered a metal hyperaccumulator, sequestering copper and zinc in fairly high concentrations (Owens et al., 1989), as well as demonstrating potential for remediation of mercury (Hg; Sinha et al., 1996), cadmium (Cd) and chromium (Cr; Rai et al., 1995; Shukla and Rai, 2007), and manganese (Mn; Sinha, 1999). Use of *B. monnieri* as a memory enhancer in traditional Indian medicine has resulted in a number of studies investigating potential active ingredients related to improved cognitive function (e.g., Deepak and Amit, 2004; Nathan et al., 2004), which has in turn sparked interest in methods for laboratory production of *B. monnieri* (Tiwari et al., 2001; Shrivastava and Rajani, 1999).

Few published studies examine the basic physiological and morphological responses of this species to common environmental stresses (but see Sinha and Saxena, 2006). The same traits that allow *B. monnieri* to cope with periodic disturbance and pollution make it a potential candidate for introduction into wetland systems that have been highly degraded, or into constructed wetland systems designed to remove pollutants. This species is an especially attractive candidate for phytoremediation and wastewater treatment, as it is already widespread throughout developing nations in tropical and subtropical regions, where the extended growing season makes such technologies practical.

We hypothesized that while *B. monnieri* is adapted to survive saturation, such conditions impose a number of constraints on nutrient sequestration including phosphorus (P) and N. The objective of this study is to examine the physiological responses of *B. monnieri* to different hydrologic regimes as an initial effort to gauge its efficacy for remediation in wetlands.

Based on previous studies in other species, two generalized responses were predicted: 1) below-ground:above-ground biomass ratios, and root penetration depth will be decreased in flooded plants, with this effect being most pronounced in the treatments with longer hydroperiods; and 2) phosphorus and N concentrations will be decreased in above-ground tissues as a result.

MATERIAL AND METHODS

Experimental design followed procedures previously described in Pierce et al. (2007). Plants were collected from wild populations found in wetland cells at the Jamie L. Whitten Plant Materials Center in Coffeeville, MS, and grown under natural light in the Life Sciences Greenhouse at the University of Memphis. Plants were grown in mesocosms 60 cm high constructed of 15 cm PVC pipe filled with a 60:40 (v/v) mixture of washed play sand and field soil, to allow for adequate drainage. Field soil was obtained from the Ap horizon of the Waverly Silt Loam Series (Soil Conservation Service, 1989). Although the high sand content of the sand/soil mixture used in this study is not representative of the soils most commonly associated with *B. monnieri*, the hydraulic conductivity of such soils is so low that achieving a well-drained control was essentially impossible given the hydroperiods under study.

After placement in PVC pipes, plants were watered and drained for a period of three weeks prior to initiation of treatments. During this time, plants were fertilized weekly with 500 mL of 20-20-20 Peter's Professional® fertilizer [N content: 3.94% ammonical (NH_4^+) N, 6.05% nitrate (NO_3^-) N, 10.01% urea N] mixed with tap water at 1.25 g/L. The pH of mesocosm effluent was measured periodically throughout the study (mean pH = 7.6 +/− 0.33). The study was terminated 56 days after treatment initiation.

Soil Moisture Treatments

Water-level was manipulated by placing mesocosms in polyethylene bags and raising or lowering the level of the bag to the appropriate distance from the top of the soil. Individual treatments were: 1) a well-watered Control allowed to drain freely (in the Control mesocosm effluent was recycled daily); 2) an Intermittently Flooded treatment that was well-watered and well-drained except on days 7, 14, 19, 28, 35, and 45, when pots were flooded to 5 cm above soil surface for a period of 48 hours.; 3) a Partially Flooded treatment with water maintained at 15 cm below soil surface. Water level within the soil was checked periodically using an internal gauge constructed from 1.9 cm perforated PVC pipe; 4) a Continuously Flooded treatment with water maintained at 5 cm above the soil surface.

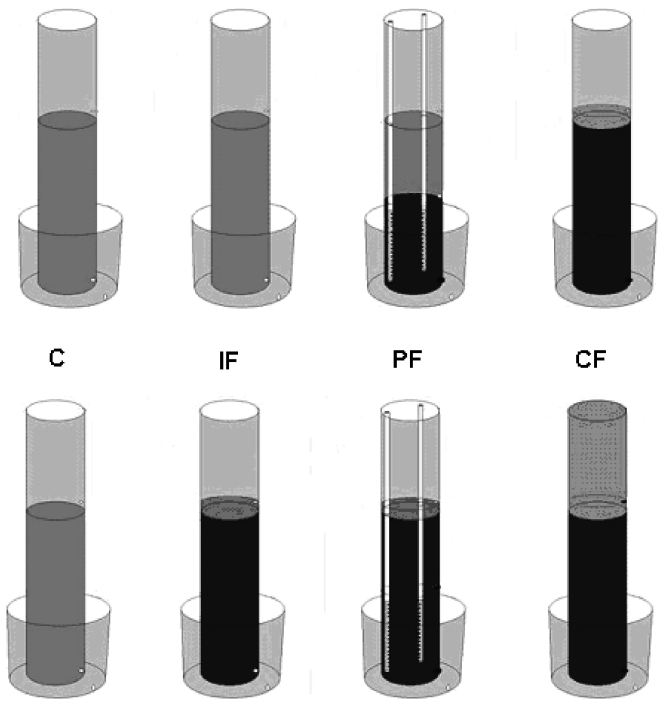

Figure 1. The top row of illustrations show water level during the main portion of the study. The bottom row of illustrations shows the same treatments during the 48-hour pulse flooding phase of the experiment, where water-level is raised to 5 cm above soil surface level in the 48-hour and partially flooded treatment, and to 20 cm above soil surface level in the saturated treatment (adapted from Pierce et al., 2007).

On days 7, 14, 19, 28, 35, and 45, Partially Flooded and Continuously Flooded mesocosms were flooded with an additional 15 cm of water for 48 hours (Figure 1).

Each treatment was replicated 12 times in a completely randomized design, with individual plants being treated as replicates. Any excess water was held in overflow buckets and used to maintain water conditions as described above. Once a week prior to the 48-hour intermittent flooding event, standing water in the three flooded treatments was drained overnight and all treatments were refreshed with seven liters of nutrient solution. The nutrient solution contained 12 mg/L ammonium nitrate and 5 mg/L sodium phosphate. These concentrations fall within the range of concentrations expected for surface flows downstream of agriculture and primary wastewater facilities (Kleinman et al., 2007; Schmidt et al., 2007; Bouldin et al., 2004; Peterson and Teal, 1996).

Soil Redox Potential

Soil redox potential (Eh) was monitored using platinum-tipped electrodes, a Model 250 A ORION redox meter and a calomel reference electrode (Thermo Orion, Beverly, MA, USA) as described by Patrick and DeLaune (1977). Redox electrodes (one at each depth) were placed at 10 cm and 30 cm below the soil surface. Measurements were replicated at least eight times per measurement day on days 0, 1, 9, 16, and 30, with measures in each pot at each depth being considered replicates.

Tissue Nutrient Analysis

Ten randomly chosen plants per treatment were analyzed for nutrient analysis. Plants were divided into above-ground and below-ground portions, air dried for two weeks, then weighed and ground in a Wiley Mill and passed through a 1 mm diameter mesh. Samples were then frozen until further processing. Subsamples of approximately 0.2 g were digested according to Quikchem Method 10-107-06-2-E (detection limit 0.018 mg/L) for Total Kjeldahl Nitrogen as described by Wendt (1997) and QuikChem Method 10-115-01-1-C (detection limit 0.015 mg/L) for total phosphorus (Lachat Instruments, 1995). The Kjeldahl digestion process stabilizes ammonium nitrogen and converts organic nitrogen into ammonium. Nitrate is not converted into ammonium. The phosphate digestion process converts organic and inorganic phosphorus to orthophosphate. Ammonium and orthophosphate were subsequently quantified by colorimetry using Lachat Instruments Quickchem FIA+ 8000 series Colorimeter.

Plant Growth and Nutrient Uptake Estimates

Immediately prior to treatment initiation, 10 plants were harvested and shoot and root lengths were measured. Plants were separated into above-ground and below-ground portions and dried in a glasshouse for two weeks, then weighed to determine biomass allocation. Nitrogen and P were measured in eight randomly chosen plants to determine initial nutrient concentrations. Initial nutrient allocation was estimated as the product of the respective biomass and concentration for each plant. The same procedures were utilized at experiment termination to compare differences in growth and nutrient allocation before and after flooding. The initial nutrient allocation values were subtracted from the final nutrient allocation values to calculate total plant nutrient uptake.

Data Analysis

Unless otherwise indicated, statistical analyses used the general linear model for ANOVA using SPSS 14, with four levels of water regime as independent fixed factors. Pairwise comparisons were made with Tukey's HSD. The Eh was analyzed using a factorial time $\times$ treatment MANOVA, with Eh values at 10 cm depth and 30 cm depth analyzed as correlated dependent variables. Due to correlation between N and P concentrations, these factors were incorporated into a single MANOVA for initial analysis, followed by univariate analysis as described above. Although N and P concentrations in the shoots were also correlated with shoot biomass, it was analyzed separately due to a larger sample size.

RESULTS

Soil Redox Potential (Eh)

Initially, Eh values were all in the range expected for aerated soils with mean at Eh = 550 +/− 73 and 585 mV +/− 56 at 10 cm and 30 cm depths, respectively. The Control treatment remained aerated throughout the study, whereas soil Eh in flooded treatments declined in response to flooding (seen as a Time X Treatment interaction, Table 1). Although soil Eh dropped in response to flooding, this response was somewhat attenuated at 30 cm depth with values stabilizing near the critical oxygen threshold (Eh = + 350 mV). The

Table 1
ANOVA table showing the main effects and interactions on Eh. Because of inherent variability in the methods used to measure Eh, a p = 0.051 for Treatment X Time interaction was considered significant for the purposes of further statistical evaluation

Effect	F	Hypothesis df	Error df	Sig.	Observed Power(a)
Treatment	12.940	6.000	208.000	.000	1.000
Time	5.604	8.000	208.000	.000	1.000
Treatment X Time	1.566	24.000	208.000	.051	.962

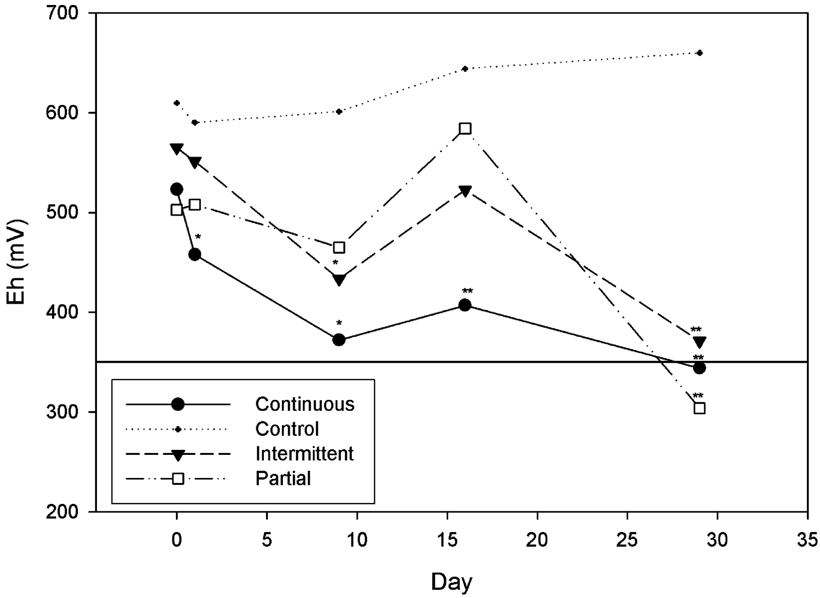

Figure 2. Soil Eh at 10 cm depth, demonstrating the variability in Eh near the soil surface. By day 30 flooded treatments were approaching Eh values that indicated soil hypoxia/anoxia. The reference line at Eh = +350 mV indicates the threshold for aerobic respiration. One asterisk indicates significant difference from the Control for a give sample date ($p < 0.05$); while two asterisks indicates a highly significant difference ($p < 0.01$).

Continuously Flooded treatment was fairly stable at 10 cm depth, with mean Eh values slightly higher than at 30 cm. Intermittently Flooded and Partially Flooded treatments had more variable soil Eh at 10 cm than 30 cm depth. By day 30, all flooded treatments were anoxic at 30 cm depth and Partially Flooded and Continuously Flooded treatments were anoxic at 10 cm depth (Figures 2 and 3).

Plant Morphology and Biomass

Mean shoot length varied from 102.6 +/− 11.34 cm in the Intermittently Flooded treatment to 89.6 +/− 11.1 cm in the Continuously Flooded treatment, but no significant differences were observed among treatments ($p = 0.099$; $F = 2.22$, $N = 48$). Root penetration depth decreased in the Partially Flooded and Continuously Flooded treatment with final penetration depth values lower than Control ($p = 0.001$ and $p < 0.001$, respectively) and Intermittently Flooded ($p = 0.006$ and $p = 0.001$, respectively; Figure 4).

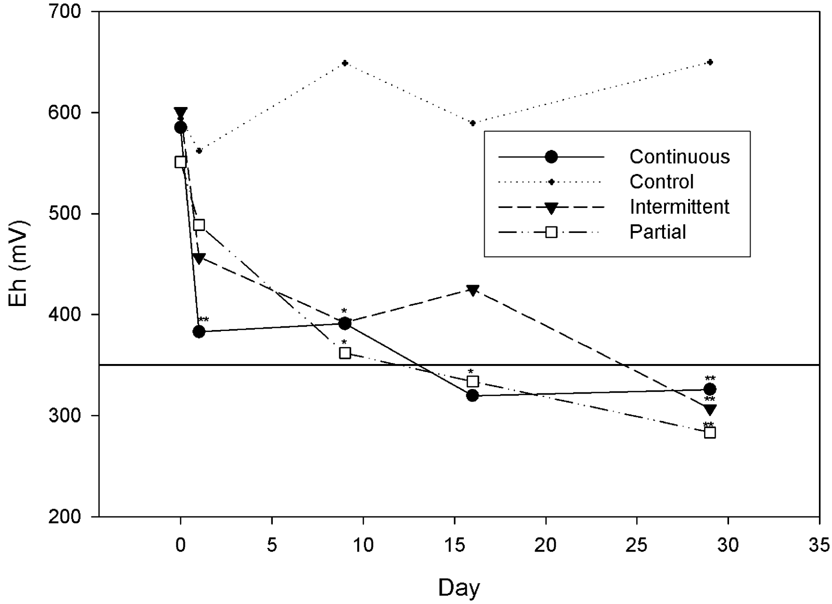

Figure 3. Soil Eh at 30 cm depth, demonstrating immediate decreases in Eh at depth, with soil reduction being somewhat attenuated over time. The reference line at Eh = +350 mV indicates the threshold for aerobic respiration. One asterisk indicates significant difference from the Control for a give sample date ($p < 0.05$); while two asterisks indicates a highly significant difference ($p < 0.01$).

Neither root biomass nor shoot biomass was significantly affected by flooding. Although root biomass increased over the duration of the study from an initial mean estimate of 1.46 +/− 2.41 (g) to a final mean value of 2.78 +/− 1.51 (g) across treatments, this difference was marginal in comparison to shoot biomass. Shoot biomass increased significantly over the duration of the study ($p < 0.001$, $F = 2.738$), with an initial mean value of 6.10 +/− 2.91 (g), compared to a final mean value of 34.2 +/− 8.9 (g).

Plant Nutrients

Mean root nutrient concentrations for N and P were 8.08 +/− 4.2 mg/g and 2.6 +/− 1.4 mg/g, respectively. They were unaffected by flooding treatments, owing to high variance within treatments. Shoot concentrations of N and P were negatively correlated with shoot mass (Pearson correlation: $r^2 = -0.366$, $N = 40$, $p = 0.02$ and $r^2 = -0.365$, $N = 40$, $p = 0.021$). Additionally, shoot concentrations of P and N were correlated with each other (Pearson correlation: $r^2 = 0.612$, $p < 0.001$, $N = 40$).

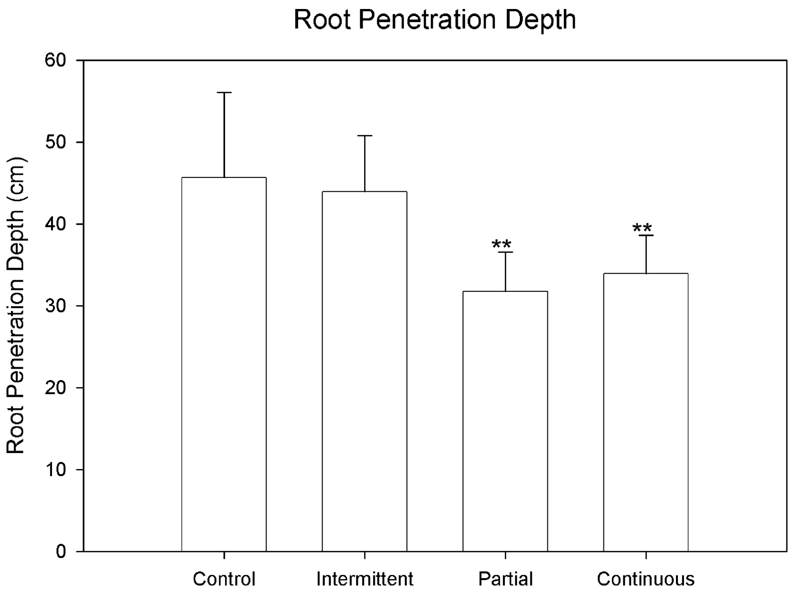

Figure 4. Root Penetration depth decreased in *Bacopa monnieri* in response to Partially Flooded and Continuously Flooded treatments, in which a stagnant water level was maintained through the majority of the study. In contrast, under the Intermittently Flooded treatment, where flooding was only short-term, root penetration was unaffected. One asterisk indicates significant difference from the Control for a given sample date ($p < 0.05$); while two asterisks indicates a highly significant difference ($p < 0.01$). Error bars are one standard deviation.

Analyzing these two variables with MANOVA resulted in a highly significant treatment effect (Hotellings trace $p = 0.006$, $F = 3.31$, $N = 40$). Shoot concentrations of N and P showed decreases in response to flooding ($p = 0.006$, $F = 4.908$ and $p = 0.005$, $F = 5.133$, respectively). Pair-wise comparisons showed that all flooded treatments differed from the Control, with the exception of shoot P in the Intermittently Flooded treatment, which was only marginally lower ($p = 0.055$; Figure 5). Nutrient concentrations were correlated to soil Eh to various degrees. For example, shoot N was only marginally correlated with soil Eh at 30 cm depth ($r^2 = 0.365$, $p = 0.065$, $N = 25$), whereas shoot P was highly correlated with soil Eh at both 10 cm and 30 cm depths ($r^2 = 0.461$, $p = 0.018$, $N = 26$ and $r^2 = 0.529$, $p = 0.007$, $N = 25$, respectively).

Uptake of N and P demonstrated a significant treatment effect ($F = 2.960$, $p = 0.050$ and $F = 4.248$, $p = 0.015$, respectively). Although all flooded treatments demonstrated lower uptake than the Control (Table 2), only in Continuously Flooded treatment was this trend statistically significant, with

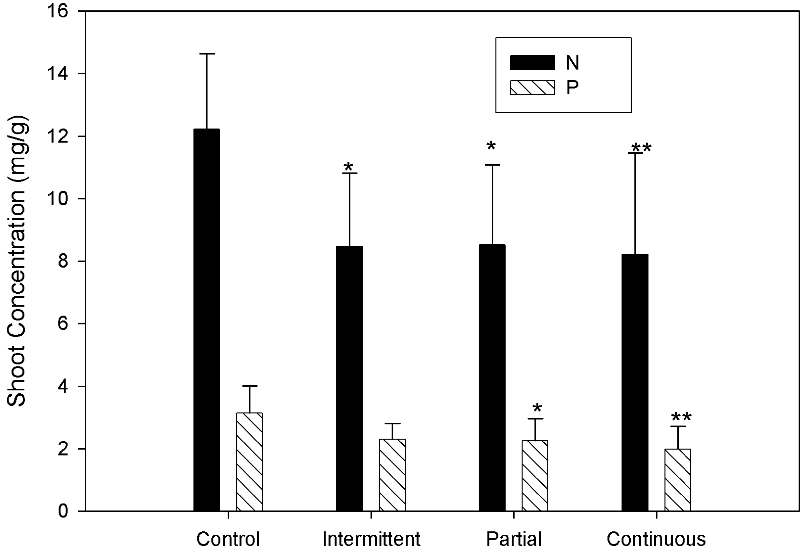

Figure 5. Shoot Concentrations of N and P in *Bacopa monnieri*. Although tissue concentration of N decreased in all flooded treatments, P concentration was not significantly reduced in the Intermittently Flooded treatment, suggesting a relationship between root length and shoot P concentration. One asterisk indicates significant difference from the Control for a give sample date ($p < 0.05$); while two asterisks indicates a highly significant difference ($p < 0.01$). Error bars are one standard deviation.

$p = 0.043$ for N and $p = 0.015$ for P. These results indicate that although Intermittently Flooded and Partially Flooded conditions influenced N and P concentrations to various degrees, total uptake was only affected by the more reducing conditions in the Continuously Flooded treatment.

Table 2

Nutrient uptake estimates of N and P for the eight week study, calculated by subtracting final nutrient content from initial nutrient content. While plant biomass increased throughout the study, nutrient concentration decreased, resulting in a net loss of nutrients in the continuously flooded treatment. Negative values in the Continuous treatment, representing net losses in N and P, may be due to partial root senescence resulting from prolonged anoxia.

Treatment	Mean N uptake (mg)	Standard dev.	Mean P uptake (mg)	Standard dev.
Control	111.4	119.4	27.3	18.0
Intermittent	15.5	51.6	6.8	16.3
Partial	40.4	70.0	14.8	23.6
Continuous	−12.5	86.1	−6.78	14.1

DISCUSSION

Control plants demonstrated moderately lower biomass than flooded treatments, a result not uncommon for wetland plants (Farmer et al. 2005; Li et al., 2004, Rubio et al., 1995). Shoot concentrations of N and P were higher in Control than in flooded plants, with mass and nutrient concentrations being negatively correlated. This relationship may be partially explained by increases in shoot mass as a sink for nutrients without a concomitant increase in root uptake capacity (Pezeshki, 2001). However, the trend toward lower plant nutrient uptake in flooded treatments suggests that flooding either decreased the availability of these two nutrients in the rhizosphere, or reduced plant uptake capacity.

Root penetration depth was affected by flooding, likely due to anoxia or reducing conditions in flooded soils. Changes in root penetration due to flooding are often related to the number of fine roots and root tips, the areas of major interface for nutrient exchange. Decreases in these absorption centers would be most pronounced for nutrients with low solubility, such as P, whereas effects on N would be probably be minimal for *B. monnieri* (Fang et al., 2007).

Previous studies in *Quercus* species have suggested that decreased nutrient uptake due to flooding could be related to decreased soil availability or reduced metabolic function (Pezeshki et al., 1999; DeLaune et al., 1998). More recent work with *Lepidium latifolium*, broad-leaf pepperweed, has demonstrated that although nutrient concentrations in roots may show no change or increase under flooding, shoot concentrations decrease, ostensibly the result of decreased apical transport as transpiration is decreased (Chen et al., 2005). Such studies generally use single leaf gas-exchange measures for comparing treatment effects on net photosynthesis and transpiration. Unpublished data on gas exchange suggests that metabolic or transpiration limitations may be related to nutrient uptake in *B. monnieri*; however, leaf morphological differences associated with flooding in this species make such inferences equivocal.

Values for soil redox potential indicated anoxic conditions developed in the bulk soil by midway through the study and persisted through the remainder of the study in the Partially Flooded and Continuously Flooded treatments. Soil reduction may have lowered N availability via a general shift in microbial activity resulting in a concurrent shift in Nitrogen transformations from NO_3^-, the nitrogen species preferred by terrestrial plants, to less available forms such as NH_4^+ or diatomic nitrogen (N_2). While *B. monnieri* acquires NH_4^+ and NO_3^- when both are present, NH_4^+ uptake, and thus total N uptake, is reduced in the absence of NO_3^- (Fang et al., 2007). In soils, as opposed to nutrient solutions such as that used by Fang et al. (2007), such effects are likely to be compounded by the cationic attraction of NH_4^+ to negatively charged soil micelles. In the present study, the possibility of reduced N uptake resulting from decreased concentrations of NO_3^- is supported by low concentrations of NO_3^- in effluent from flooded mesocosms (<1 mg/L, unpublished data).

Phosphorus is relatively insensitive to redox changes, but availability to plants is often inversely related to redox potential. Soil reduction dissociates insoluble metal-phosphate complexes, often resulting in an increase in plant-available Phosphorus. (Vepraskas and Faulkner, 2001; Gambrell and Patrick, 1978). Therefore, although decreases in plant tissue concentrations of N may be directly related to changes in plant availability, Eh is unlikely to directly increase the availability of P. The pH is known to affect plant available P, with alkaline conditions being generally unfavorable for P uptake. The pH values measured from mesocosm effluent were greater than pH = 7.2, indicating conditions of low plant available P. However, as these pH conditions were measured in effluent, rather than derived from rhizosphere soil samples, they are probably not accurate representations of the root environment. This disparity may be especially true for *B. monnieri*, as it exudes substantial amounts of protons into the rhizosphere, resulting in rhizosphere acidification (Fang et al., 2007). The manner in which such root exudates affect soil environments is complex, often involving feedback between soil microorganisms and chemical conditions; however, if decreases in pH of the bulk soil result from proton exudation into the rhizosphere, the solubility of metals as well as phosphate (PO_4^-) would be expected to increase. It is unclear to what degree rhizosphere acidification in *B. monnieri* is related to its ability to sequester metals.

Future studies examining nutrient relations in wetland plants exposed to soil reduction must simultaneously examine multiple mechanisms in order to adequately explain plant response. These mechanisms include changes in assimilation rates due to either soil nutrient availability (e.g., NO_3^- versus NH_4^+) or plant metabolic limitations to nutrient uptake, changes in the root:soil interface, and changes in translocation of nutrients to shoots. The decreased concentrations of N and P in flooded treatments may be indicative of a general trend toward decreased shoot translocation of minerals in this species, and should be considered for further study, particularly with regard to industrial applications where metal uptake is a key factor. Further understanding of nutrient relations in *B. monnieri* may elucidate how this plant functions as a metal hyperaccumulator, as well as management practices to increase its efficacy in soil and water amelioration, in particular under dynamic hydrologic conditions commonly found in agricultural ditches and urban stormwater runoff.

CONCLUSIONS

Hydrology in managed wetlands is important not only in relation to hydraulic retention time and soil reduction, but also indirect effects on plant physiology. Flooding decreased shoot tissue concentrations of N and P in *B. monnieri* to varying degrees, while increasing shoot biomass. Increased biomass only partially explained flooding effects on nutrient concentrations, as calculated values for nutrient uptake were decreased only in Continuous Flooding. Decreased N availability resulting directly from soil reduction in flooded treatments may have affected N uptake, whereas changes in root morphology likely played a part in tissue nutrient concentration differences. This study suggests that although *B. monnieri* is commonly found in aquatic environments, the resulting soil reduction can result in decreased mineral uptake. In environments where plant uptake of nutrients represents a significant portion of the overall mineral immobilization, the need for increased hydraulic retention time should be weighed against the potential stresses on emergent plants. In cases where *B. monnieri* is used for metal phytoremediation of terrestrial sites, inadequate drainage may result in decreased efficacy.

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